

# DIVERSITY IN THE FUNCTIONAL ORGANISATION OF THE MANDIBULAR STYLETS OF ASSASSIN BUGS (HETEROPTERA: REDUVIIDAE)<sup>1</sup>

(With eight Plates)

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**Key words:** Assassin bugs, non-tibiarolate, tibiarolate, Reduviidae, mandibular stylets, mandibular lever, evolution.

Nine years of intensive survey of assassin bugs in southern India yielded 171 species belonging to 65 genera and 11 subfamilies. Diversities in the functional organisation of the mandibular stylets of 77 species of Reduviidae, representing 45 genera and 11 subfamilies of non-tibiarolate and tibiarolate groups of Reduviidae viz., Harpactorinae, Stenopodainae, Emesinae, Saicinae, Holoptilinae, Tribelocephalinae, Acanthaspidinae, Salyavatinae, Ectrichodiinae, Piratinae and Triatominae, collected from all the four major ecosystems (Tropical Rain Forest, Scrub Jungles, Semi-arid zones and Agroecosystem) have been critically assessed. The mandibular stylets of all Reduviidae are isomorphous, with the exception of Holoptilinae. The spatulate mandibular stylets of the myriophagous Ectrichodiinae appear to be specialised for sawing apart the septa between the segments of their prey. Depending on the feeding strategy and nutritional ethology, the organisation of the denticles present at the tip of the mandibles varies considerably. This is considered here as the main criterion for the assessment of their evolutionary significance in the various species of Reduviidae occupying diverse ecosystems. Careful observation of the shape of the mandibular lever and its significance in the evolution of the functional organisation of the stylets has been recorded.

## INTRODUCTION

In Reduviids, the stylet fascicle is composed of a pair of outer mandibular stylets and a pair of inner maxillary stylets, all four of them being collectively involved in piercing and sucking operations. While the mandibular stylets are primarily responsible for piercing and anchoring, the maxillary stylets are responsible for the ejection of the saliva into the substrate through the dorsal salivary orifice and ingestion of semidigested fluid through the ventral food orifice.

The mandibular stylets, representing the incisor of the mandibles of a generalised insect, on either side of the maxillary stylets, embrace the latter and function in a groove and ridge

sliding principle. Each mandibular stylet, at its base inside the head capsule, is connected to the mandibular plate of the head capsule by a highly sclerotized triangular plate called the mandibular lever. The detailed morphology of the mandibular stylets and their lever in several families of Heteroptera are known from the works of Parsons (1959, 1962, 1968 and 1969), Livingstone (1968 and 1969) and Cobben (1978).

Depending on the feeding strategy, the organisation of the denticles at the tip of the mandibles varies considerably and that is considered here as the main criterion for assessing their evolutionary significance in the various species of the Reduviidae, occupying diverse ecosystems.

In the present study, mandibular stylets of 77 species, representing 45 genera and 11 subfamilies of both non-tibiarolate and tibiarolate groups of Reduviidae from different

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ecosystems of southern India have been critically assessed.

#### MATERIALS AND METHODS

Materials were obtained from dried and preserved Reduviid specimens. The heads were boiled in 5% potassium hydroxide solution for upto 10 minutes, depending on the intensity of pigmentation, washed in weak acetic acid and again washed thoroughly in water and stored in glycerine for better clarity. The dissected materials were cleared in clove oil and mounted in polyvinyl lactophenol. Photomicrographs under light microscope were taken with Asahi Pentax photomicrographic equipment.

#### OBSERVATIONS

##### I. Non-tibiaroliolate group of Reduviidae

The mandibular stylets in 42 species belonging to 26 genera and 6 subfamilies of non-tibiaroliolate reduviids examined show complete isomorphism in all the subfamilies, except in the Holoptilinae in which they are dimorphic and asymmetrical. Each subfamily has certain common characters for all the genera and species, with regard to the number and disposition of longitudinal striations and arrangement of transverse denticulate serrations.

Apically, the mandibular stylets are acutely drawn out in the form of a spike and the nature and development of their denticulate serrations vary considerably. In the Harpactorinae, three longitudinal rows of such serrations are found, in which the outer rows, as in *Rhinocoris kumarii*, all *Coranus* species, both species of *Irantha* and *Polididus armatissimus* (Pl. 1, figs. 4; Pl. 2, figs. 14, 16, 17, 20, 21 & 22), are provided with three sharp, backwardly directed denticles which are not connected by transverse ridges. In the case of *Rhinocoris marginatus*, *R. longifrons*, *R. fuscipes*, *Euagoras plagiatus*, *Endochus cingalensis*, *E. inornatus*, both species of *Sycanus*, *Platerus bhavanii*,

*Neohaematorrhophus therasii* and *Macracanthopsis nigripes* (Pl. 1, figs. 1, 2, 3, 6, 7, 8, 9, 10; Pl. 2, figs. 13, 18 & 19) all the three rows are not interconnected by transverse serrations. In the case of *Polididus armatissimus* (Pl. 2, fig. 22) however, the two outer rows are distinctly connected by a transverse ridge without a median longitudinal row of denticulate serrations. In *Lanca kandyensis* (Pl. 2, fig. 12) these serrations are more prominently developed upto the apex, whereas in other species the more apical ones are not prominent.

In *Lophocephala guerini* (Pl. 1, fig. 5) the stylets are more membraneous except at the edges that carry prominent denticulate serrations more apically drawn into sharply pointed spikes. The stylets of all *Coranus* species are relatively narrow. In both *Rhaphidosoma* species (Pl. 3, figs. 25 & 26) the mandibular structures are entirely different from the other harpactorine species, and are more like those of the Stenopodainae in having about five to six longitudinal rows, with acutely pointed denticles at the apex. The outer rows are very sharply developed, pointing backwards. In both species of *Cydnocoris* (Pl. 2, fig. 23; Pl. 3, fig. 24) the mandibles have completely deviated from the harpactorine type, being spatulate, apically bearing three obscure rows of denticulate serrations, not connected to each other by transverse ridges.

In the Stenopodainae species like *Oncocephalus chamundaii*, *O. impudicus*, *O. klugi*, *O. cingalensis*, *O. annulipes* and *O. schioedtei* (Pl. 4, figs. 39, 40, 41, 43, 44 & 45), the mandibular stylets are uniformly similar in the arrangement of their denticulate processes. More basally, there are about 10 longitudinal rows of denticles and the number gradually diminishes apically from 4 to 1. It appears that the denticulate processes abruptly end at the posterior border of the serrated area, behind which the serrations gradually vanish. In *Canthesancus picticollis* (Pl. 4, fig. 46) the denticulate processes are much more



prominently developed and many more transverse ridges are found.

In the case of *Bardesanes sericenotatus*, *Diaditus errabundus*, *Pygolampis foeda*, *Staccia diluta*, *Caunus farinator* and *Oncocephalus notatus*, (Pl. 3, figs. 33, 34, 35, 36; Pl. 4, figs. 37 & 38), the longitudinal rows are less in number, but the denticles are more powerfully developed.

In Emesinae, the mandibular stylets are acutely pointed apically. In *Stenolaemus susainathani* and *Ischnobaenella naraikkadu* (Pl. 4, figs. 47 & 48), the denticulate processes are obscure and developed in the form of more transverse ridges. About 18 to 24 such ridges are found.

The mandibular stylets of Saicinae (*Polytoxus maculatus*) (Pl. 3, fig. 31) are similar to those of Emesinae in shape, having similar rows of ridges.

The mandibular stylets of Holoptilinae (Pl. 3, figs. 27 & 28) differ from all other species in being dimorphic. Both stylets are spatulate. The right one differs from the left one in being boat-shaped with longitudinal striations. Apically, it is acutely pointed, its surface forming a keel.

In Tribelocephalinae (*Tribelocephala indica*) (Pl. 3, fig. 30) interestingly, the mandibular stylets do not have any serration but they are boat-shaped and apically pointed.

The mandibular lever in non-tibiarolate reduviids is consistently present in all species examined and it is roughly triangular with minor variations in shape and size. While in Harpactorinae (*Sycanus collaris* and *Coranus atricapillus*) (Pl. 1, fig. 11; Pl. 2, fig. 15), Holoptilinae (*Holoptilus melanospilus*) (Pl. 3, fig. 29) and Saicinae (*polytoxus maculatus*) (Pl. 3, fig. 32), one side of the lever is more elongated. In the case of Stenopodainae (*Oncocephalus klugi*) (Pl. 4, fig. 42) the three sides are almost of the same length. The size of the lever appears to vary according to the size of the insect.

From the foregoing account it appears that among the Harpactorinae, the *Rhinocoris*, *Irantha*, *Euagoras*, *Macracanthopsis*,

*Neohaematorrhophus*, *Platerus*, *Sycanus*, *Endochus*, *Lanca* and *Coranus* have a more or less similar arrangement and development pattern of denticulate serrations. In all these genera all the three rows are not transversely connected and there is gradation in the development of denticulate processes of these serrations.

*Lophocephala guerini*, *Rhaphidosoma atkinsoni*, *R. tuberculatum* and the two species of *Cydnocoris* are markedly different from all other species of Harpactorinae examined. In Stenopodainae, all the species of *Oncocephalus* are virtually similar in their identity. The mandibular stylets of *Staccia*, *Oncocephalus notatus*, *Diaditus*, *Pygolampis* and *Caunus* have closer affinity with one another. *Canthesancus* and *Bardesanes* are also similar. The similarity of the mandibular stylets of the Emesinae and Saicinae (*Polytoxus*) is very significant.

Mandibular stylets of the Tribelocephalinae, by their boat-shaped structure, appear to be unique among Reduviidae and the characteristic asymmetry of the mandibular stylets of Holoptilinae could be also considered as a unique feature among Reduviidae.

## II. Tibiarolate group of Reduviidae

Studies on 35 species representing 19 genera and 5 subfamilies of the tibiarolate group of Reduviidae of southern India confirmed that both mandibular stylets in all these species are perfectly symmetrical and isomorphic. The denticles of the serration, however, vary in their number and extent of development.

In Acanthaspinae, all species examined have three longitudinal rows of serrations, but the development of the denticles in the transverse rows varies considerably. The more slender and acutely pointed the mandible is, the more sharply defined are the denticles of the transverse rows, as in *Acanthaspis siva*, *A. quinquespinosa*, *A. angularis*, *A. rugulosa* and *A. lineatipes* (Pl. 6, figs. 63, 64, 65, 66 & 68). In *Reduvius delicatula* (Pl. 7, fig. 75) the mandibular stylets are more



sharply defined than in other species in which mandibles are not very acutely pointed apically and their denticles are not so sharply defined, as in *Acanthaspis pedestris* and *A. siruvanii* (Pl. 6, figs. 62 & 67). In *Apechtia mesopyrrha*, *Pasira perpusilla* and *Neoacanthaspis maculatus* (Pl. 6, figs. 70, 71; Pl. 7, fig. 77) the stylets are broad and bluntly pointed and their apical transverse denticles just moderately developed. In *Apechtia mesopyrrha* and *Pasira perpusilla* they are significantly poor in their formation. However, in these two species the stylets carry certain minute backwardly directed serrations, far behind the apex and they are better pronounced in *Pasira perpusilla* (Pl. 6, fig. 72). In *Edocla slateri* and *Edocla maculatus* (Pl. 7, figs. 73 & 74) the mandibular stylets are similar in the development of their denticles along with the three longitudinal rows. In *Platymenis laevicollis* (Pl. 7, fig. 76) also, the serrations are arranged in three longitudinal rows.

In Salyavatinae, the denticles are arranged in three rows but unlike Acanthaspidinae, the three rows are not transversely connected. However, a slight indication of the same is seen in *Nudiscutella frontispina* (Pl. 5, fig. 59) and *Lisarda annulosa*. (Pl. 5, fig. 58). The posterior edge of the stylets, far behind the apical rows of the denticles, is sharply serrated. These serrations are directed forward in *Petalochirus brachialis* (Pl. 5, fig. 60). In *N. frontispina* such serrations are ill-defined. The denticles in all the three rows are equally well formed, and better defined than those of Acanthaspidinae.

In Ectrichodiinae all the four species of *Ectrychotes*, namely, *E. dispar*, *E. pilicornis*, *E. bharathii* and *E. atripennis* (Pl. 5, figs. 49, 50, 51 & 52), have mandibular stylets almost abruptly expanding beyond the middle, whereas in *Labidocoris elegans*, *Haematorrhophus nigroviolaceous* and *Stegius pravus* (Pl. 5, figs. 53, 54, 55 & 56) such expansion is gradual. Such a mandibular stylet in Ectrichodiinae is unique in being spatulate without any trace of denticulate serrations, unlike all other species

of tibiariolate group of Reduviidae.

In Piratinae, each of the four genera examined show significant variation. In general, most of the *Ectomocoris* species, namely *E. tibialis*, *E. tuberculatum*, *E. quadriguttatus* and *E. cordiger* (Pl. 7, figs. 80, 81, 82 & 83), have six longitudinal rows of serrations at the base of the denticulate areas of the stylet, of which the denticles of the outermost rows are more sharply defined. There are about eleven such denticles on the two peripheral longitudinal rows. In *Catamiarus brevipennis* and *Sirthenia flavipes* (Pl. 8, figs. 90 & 91) as well as in all other *Pirates* species, there are about four distinct longitudinal rows of serrations. In *C. brevipennis* (Pl. 8, fig. 90) they are better defined than in the others. While all the four species of *Pirates* namely *P. affinis*, *P. quadrinotatus*, *P. lepturoides* and *P. atromaculatus* and in *C. brevipennis* (Pl. 8, figs. 85, 86, 87, 88 & 90), the more apical denticles are flattened and less conspicuous. In *Sirthenia flavipes* (Pl. 8, fig. 91) the more apical ones are highly conspicuous and sharply developed.

In Triatominae, the stylet tip is sharply pointed, there is only one series of sharply defined denticles and about eight such prominent denticles could be recognised. Among all the tibiariolate reduviids examined, *Triatoma rubrofasciata* (Pl. 7, figs. 78 & 79) has the maximum development of mandibular stylet. It is the only haematophagous reduviid examined.

Thus, among all the 36 species of tibiariolate reduviids examined, *Triatoma rubrofasciata* has the most specialised mandibular stylets and *Pirates* sp. have the least developed stylets. Acutely pointed mandibular stylets are met with in the alate group of Acanthaspidinae. It is observed that *Ectomocoris* has more specialised mandibular stylets compared with other genera of Piratinae and the genus *Acanthaspis* is considered to be most specialised when compared with all other genera of Acanthaspidinae. Interestingly, the alate



species of *Acanthaspis* have better developed mandibular denticles than their apterous counterparts. Members of the subfamily Ectrichodiinae have attained a unique type of specialization for myriophagy.

The mandibular lever, as revealed in a number of species of tibiarolate reduviids in the present investigation, is roughly triangular with perceptible variation in its size. The lever of Acanthaspidinae (*Acanthaspis pedestris*) (Pl. 6, fig. 69), Piratinae (*Ectomocoris cordiger* and *Pirates atromaculatus*) (Pl. 7, fig. 84; Pl. 8, fig. 89) Ectrichodiinae (*Haematorrhophus nigroviolaceus* (Pl. 5, fig. 57) is more or less similar, but for minor variations in the development of their angles. The lever of Salyavatinae (*Lisarda annulosa*) (Pl. 6, fig. 61) is different from all others in being very tiny and T-shaped. It is larger in Ectrichodiinae.

#### DISCUSSION

The structure of the mandibular stylets of Reduviidae manifests a wide range of variations and provides sufficient evidence to trace the course of evolution of carnivory in these insects. In the phylogenetic relationship within subfamilies, however difficult it may be to establish, each subfamily presents a wide range of parallel evolution in stylet structures.

The fact that Holoptilinae alone, among all other Heteroptera, present dimorphism in mandibular stylets, as reported by Cobben (1978) and confirmed by the present investigation, suggests that Holoptilinae could be regarded as an early offshoot from the Reduviid stem. Emesinae and Saicinae closely resemble each other in having more conspicuously tapered needle-like mandibles. This tendency to taper is indicated in the mandibular stylets of the Stenopodainae as well. In *Lophocephala guerini* (Phonolibinae) as well as in Rhaphidosominae, the mandibles are more acutely pointed since both of them have termites as their staple prey, and

probing for termites underneath dried faecal material (Livingstone and Ambrose 1984) is mainly achieved by the mandibular stylets.

A comparison of mandibular stylets of species of the three major categories of carnivory in Reduviidae, namely myriophagy, haematophagy and entomophagy, represented by Ectrichodiinae, Triatominae and the rest respectively, provides valuable information on the nutritional strategies of these bugs in their respective ecosystems in particular, and their evolutionary significance in general. The development of a single series of highly denticulate serrations on an extremely slender mandibular stylet of Triatominae could be interpreted as an efficient piercing mechanism, over a highly sensitive host skin. According to Lavoispiere *et al.* (1959), in *Triatoma*, entry of the stylets into the host skin is very rapid, initiated by alternating movements of the mandibular stylets which, after having penetrated into the tissue of the host, remain still and the maxillary stylets project far beyond the mandibles, as a single bundle.

The blade-like, sharp edges of the spatulate type of mandibles of Ectrichodiinae can easily saw the septa between the segments of millipedes, once the stylet fascicle has established entry through the intersegmental membrane. A spatulate mandibular stylet has the advantage of advancing deeper inside the host's body rather than anchoring alone. According to Cobben (1978), it might be the beginning of evolution of a functional relationship in which the mandibles control deviation of the maxillary bundle. A close relationship with the mandibles of myriophagous species of Ectrichodiinae is recognized only in both species of *Cydnocoris* that exhibit a sharp deviation from the normal condition of mandibular stylets in all other entomophagous species. However, both species of *Cydnocoris* have been found to feed freely on houseflies in the laboratory.

Harpactorinae, in general, have their mandibular stylets neither acutely pointed as in



Emesinae nor spatulate as in Ectrichiinae, though Cobben (1978) has described the mandibles of both Harpactorinae and Ectrichiinae as spatulate. In Tribelocephalinae, which feed mainly on termites, the mandibular stylets appear to be intermediate between Emesinae and Harpactorinae. Most species of Harpactorinae are polyphagous, whereas ant-feeding Holoptilinae and termite-feeding Phonolibinae (*Lophocephala*), Rhaphidosominae and Tribelocephalinae tend to be monophagous. Hence it was easy to rear Harpactorine species on different hosts and it is difficult to rear all other species that feed exclusively on termites.

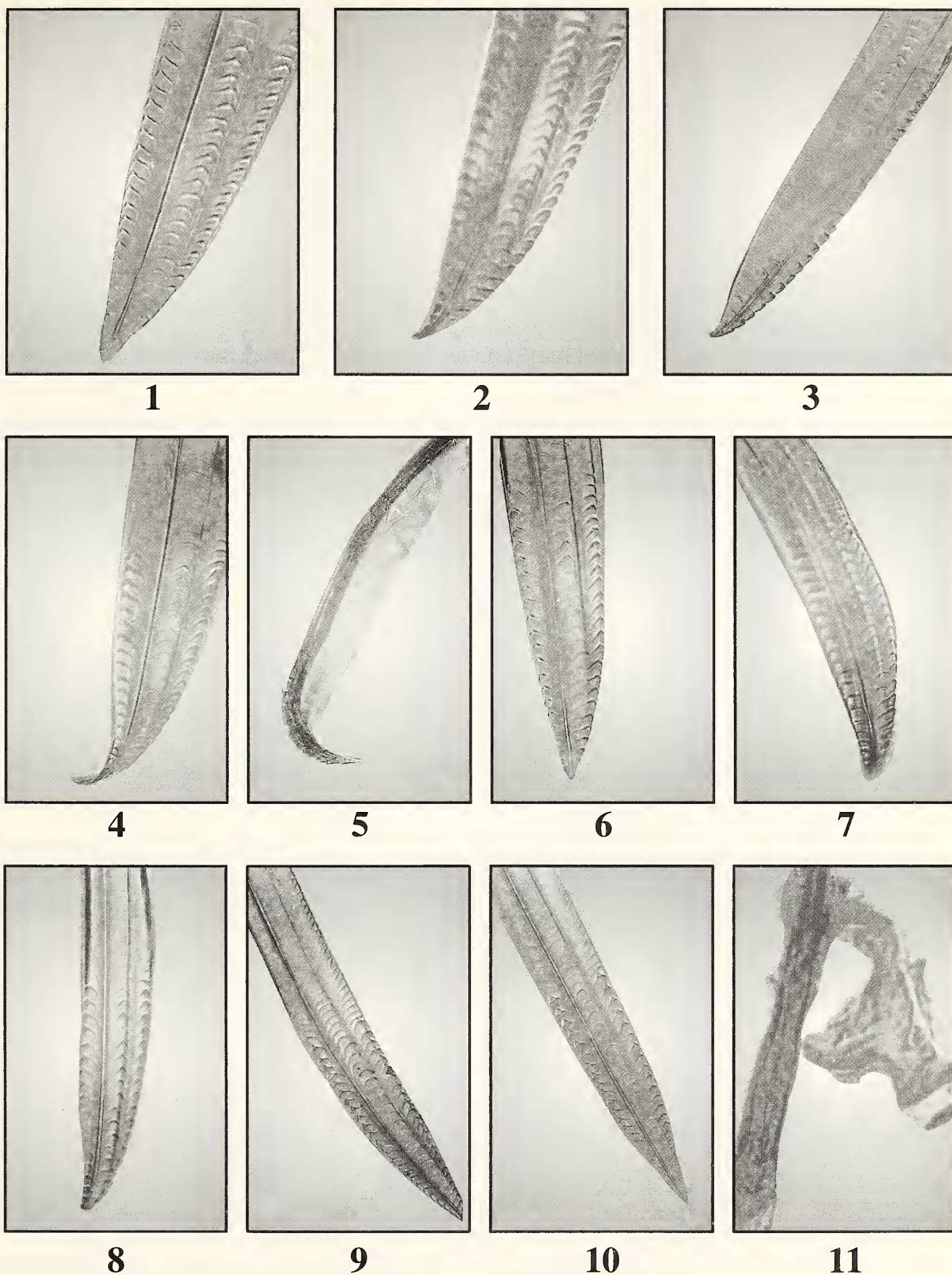
The development of serrations with denticulate processes, at the tip of mandibular stylets appears to be common in all the species except *Tribelocephala* in which they are obscure and rarely found, and it is apparently difficult to attribute predatory efficiency based on the manner of development of such serrations in the mandibular stylets of Reduviidae. However, it is evident that the shape of the mandibular stylets and their armature in most cases are directly related to the nature of predation of their natural prey. The evolution of mandibular stylets, therefore, could be correlated with the prey and feeding strategies.

In the entomophagous group, the development of a greater number of rows of denticulate serrations was considered as a more efficient predatory device, amply illustrated by *Ectomocoris*, that could be considered as one with a more efficient mechanism of predation. Cobben (1978) is of the opinion that the mandibles became increasingly flattened and extensively sculptured with the evolution of phytophagy from carnivory. The mandibles in phytophagous species serve initially as a piercing device, and once penetration is achieved they serve as an anchoring device. Since the tibiaorium of *Ectomocoris* has reached the maximum development among the tibiarolate group of Reduviidae (Livingstone and Ambrose,

1984) the mandibular armature may be considered as an additional attribute towards efficiency in predation. However, reduction of armature of any form in an appendage, especially the stylets, is an apomorphic feature and for that reason the multiplicity of denticulate serrations in *Ectomocoris* could be regarded as a plesiomorphic feature among the tibiarolate Reduviidae. According to Cobben (1978), a larger mandibular lever is correlated with the curved base of the stylet, allowing greater force and striking velocity during harpooning of the prey. It allows torsion of the mandibular stylet by the action of the sets of muscles. A quadrangular mandibular lever, commonly reported in *Gerromorpha* (Ekblom, 1926 & 1930; Elson, 1937; Spooner, 1938; Servadei, 1946; Parsons, 1962 and Cobben, 1978) has been considered as an autogenic transformation from a normal triangular lever in the nymphal instars, and according to Cobben (1978) such a type is the IVth type of lever that provides the mandibular stylet with greater rapidity and force in harpooning. A triangular type is the type II of Ekblom (1926) and in the present study the lever could be rated as an intermediate one between type II and type IV. The larger size of the triangular lever in Ectrichiinae could be correlated with the unusual spatulate shape of the stylet that aids in sawing the intersegmental septa of the myriapod prey. Therefore, it is suggested that myriapod feeding is a remarkable line of specialization achieved by the Ectrichiinae alone.

According to Cobben (1978), the mandibles become increasingly flattened and extensively sculptured with the evolution of phytophagy from carnivory and the increased capacity to protrude the mandibles arose independently in Reduviidae, Nabidae and Anthocoridae. It is suggested that the mandibular stylets initially serve as the anchoring device, enabling the maxillary stylets to perform exploratory movements inside the host tissue, preparatory to feeding.





Figs. 1-11: 1. *Rhinocoris marginatus* Laporte (200 x); 2. *Rhinocoris longifrons* Stal (400 x); 3. *Rhinocoris fuscipes* Fabricius (400 x); 4. *Rhinocoris kumarii* Ambrose & Livingstone (400 x); 5. *Lophocephala querini* Laporte (400 x); 6. *Euagoras plagiatus* Burmeister (400 x); 7. *Endochus cingalensis* Stål (400 x); 8. *Endochus inornatus* Stål (400 x); 9. *Sycanus pyrrhomelas* Walker (200 x); 10. *Sycanus collaris* Fabricius (200 x); 11. *Sycanus collaris* Fabricius (mandibular lever) (200 x).